

NERVOUS INTEGRATION IN THE FACET EYE

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INTRODUCTION

An investigation of nervous integration in the faceteye can in principle be carried out in two different ways. In the first approach a quantitatively measurable response of the whole animal to optical stimulations is recorded and the "input-output" relations analyzed in terms of a minimum mathematical model. This approach leads to a theory for the part of the Central Nervous System involved in the reaction and enables us to understand the principles of information processing taking place. The second approach is based on electrophysiological techniques. The registration and evaluation of evoked retinula cell and nerve cell potentials allows one to draw conclusions about the principles of interaction taking place in the optic nerve system. This paper deals mainly with the first approach. It will be concerned with an analysis of optomotor responses in insects. In the second part of the paper, however, some of the consequences of lateral inhibition in faceteyes will be discussed.

PERCEPTION OF OPTICAL MOVEMENT IN INSECTS

Many animals react to the perception of optical movement by turning their eyes, the head and finally often their whole body. This response to seen movement is called optokinetic reaction. It is a graded response to the moving stimulus.

Figure 1 illustrates how optokinetic reactions can be elicited (Hassenstein and Reichardt, 1956a, b, 1959): The experimental animal, the beetle *Chlorophanus* sits inside a cylinder with vertical black and white stripes. If the cylinder is rotated, the animal tries to follow the seen movement. It reduces the relative speed between the environment and itself. Environment and animal—considered as a unit—form a feedback loop.

The experimental set-up illustrated in Fig. 1 does not permit quantitative assessment of the optokinetic reaction. Through its own movements the animal continually changes the moving stimulus which acts upon its eyes. Fig. 2 shows how the beetle can be prevented from moving in relation to the experimental arrangement without depriving it of its capacity for optokinetic reactions (Hassenstein 1951). A piece

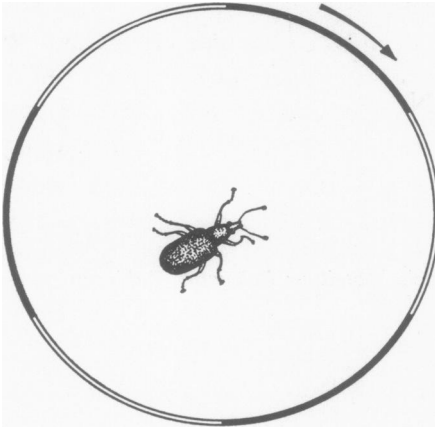


FIGURE 1 The beetle *Chlorophanus* follows the direction (arrow) of the turning cylinder. Note posture of antennae and legs.

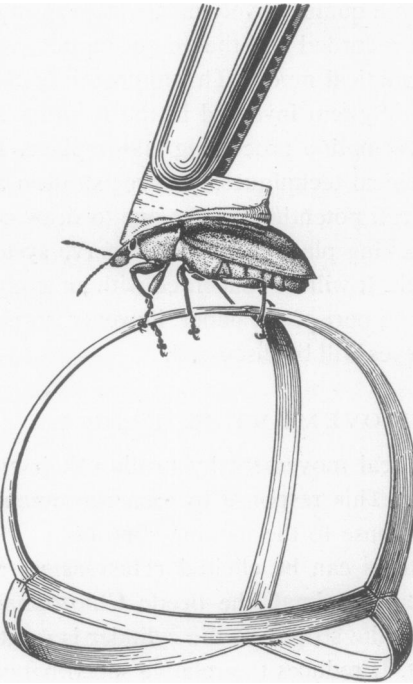


FIGURE 2 The beetle *Chlorophanus viridis* glued to a small piece of cardboard and suspended from a pair of tweezers carries a straw sphere (weight: 30 mg) by its own effort. Neck and head are also fixed. As soon as the animal begins to walk the straw sphere rotates underneath. With every few steps the animal has to choose between two paths. The strength of its turning reaction is manifested by the proportion of right and left choices while the beetle remains stationary.

of cardboard is glued to the carapace of the experimental animal. A pair of tweezers holds the cardboard and in this way the animal. The beetle is hanging freely in space. In this position it is given a sphere fashioned of straw which it holds voluntarily; the straw sphere is just as heavy as the beetle itself; it does not carry an unusual weight; it supports its own body weight, as if crawling upside-down along the underside of a leaf. The straw sphere is constructed in such a way that the six

component straws meet at four points forming three angles of 120° each. As the beetle engages in crawling movements the straw sphere rotates underneath. With every few steps the beetle arrives at a Y-shaped fork—or, more precisely, the fork reaches the beetle. The beetle must decide to turn to the right or left. Obviously, these choices do not change the position of the animal, since it is rigidly suspended by its back; yet the choices demonstrate to the observer the strength of the animal's turning tendency. After every choice the beetle is in the same position as before ready for the next choice. The important point is that the choices made by the beetle on the straw sphere are influenced by the moving stimulus in exactly the same manner as are the animal's movements on the plane surface. Normally, i.e., in the absence of a moving stimulus, the beetle turns equally often to the right and to the left while crawling on the straw sphere. However, under continuous stimulation eliciting a tendency to turn toward the right the proportion amounts, e.g., to 55 choices to the right compared with 45 to the left. Since this proportion depends clearly on the strength of the optokinetic reaction, we can introduce the quotient

$$R = \frac{W - A}{W + A}$$

as an appropriate measure of reaction. W indicates the number of choices "with" and A the number of choices "against" the direction of the rotating cylinder. Statistical considerations demonstrate that R represents a linear measure for the strength of the turning reaction if the proportion $(W - A)/(W + A)$ does not exceed 0.7 (Hassenstein, 1958, 1959). Hence, measurement of the reaction has been limited to the range $-0.7 \leq R \leq +0.7$.

The method of using the straw sphere removes from the optokinetic reaction any uncertainty caused by actual locomotion of the beetle; it also makes the reaction susceptible to quantitative measurement. In our experiments the moving stimulus is exposed long enough to allow the beetle to make as many choices as are needed for a statistically significant measure of the turning reaction, in terms of the proportion of choices in any case.

In the experimental arrangement of Fig. 2 the feedback loop formed by animal and environment in Fig. 1 is cut off. Under these circumstances direction and strength of optokinetic reaction become indicators of the perceptual processes which take place in the central nervous system of the beetle while it perceives movement.

Man sees motion not only upon presentation of continuous movement, but also on quick succession of stable images. This also holds for insects whose eyes are composed of individual units (ommatidia). Light flashes arranged in a row and appearing at short intervals elicit in insects the same optokinetic reactions as does continuous movement. This has its advantages for the study of motion perception: the presentation of the stimulus can consist of small discrete light stimuli arranged in a systematic fashion, e.g., the "on" and "off" of a single light source.

Fig. 3 shows an example of an experimental arrangement that has been used for various quantitative tests (Hassenstein 1958b): The arrangement consists of three concentric cylinders; during the experiment the beetle with the straw sphere is placed in the center. The cylinder nearest the center has vertical slits and is stationary. The outside cylinder has broad black and white stripes. They are arranged in such a fashion that—seen from the center of the cylinders—the slits of the inner cylinder expose alternating white and black fields.

Between the outer and the inner cylinder is a rotating cylinder consisting of gray sectors. When that cylinder rotates, the leading and the trailing edges of its sectors produce successive changes of illumination in the slits of the innermost cylinder. Specifically, the movements of the rotating cylinder produce the following sequence of luminous stimuli for the eyes of the beetle: if one designates increase in light with +, darkening with −, and a series of neighboring slits with X, Y, Z, \dots , then the experimental arrangement in Fig. 3 yields the following sequence (starting with a

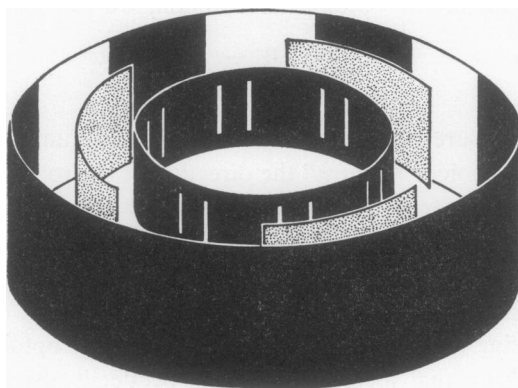


FIGURE 3 Example of an experimental arrangement for the production of a series of light changes. The arrangement consists of three concentric cylinders; the beetle with the straw sphere is placed in the center. The inner cylinder is stationary; it is a cylinder with vertical slits. The outer cylinder does not rotate either; it is the background cylinder. In this particular case, black and white fields are arranged on the outer cylinder in such a fashion that—seen from the center each pair of slits exposes one white and one black field as a background. Between the inner cylinder and the background cylinder is the rotating cylinder composed of three separate gray sectors.

+ stimulus): + in X , − in Y , + in $Z \dots$ and then, after a pause, − in X , + in Y , − in Z , etc. With similar experimental arrangements it is possible to produce nearly any series of changes in illumination and to stimulate the ommatidia of beetles accordingly.

If we designate adjacent ommatidia in a horizontal section of a compound eye with A, B, C, D, E, \dots the sequence of, say, light stimuli in adjacent ommatidia A and B can be expressed as $S_{AB}^{++}(t_1, t_2)$. The first stimulus is received by om-

matidium A at the time $t = t_1$; the second stimulus by ommatidium B at the time $t = t_2$. The response of the animal to this stimulus combination can be symbolized by $R_{AB}^{++} (t_1, t_2)$.

Expressed in this symbolism the following experimental results can be reported:

(a) Two light stimuli following each other in two ommatidia form the most elementary stimulus sequence capable of eliciting optokinetic reactions.

(b) Two stimuli which impinge on one and the same ommatidium are ineffective for motion perception; equally without effect are pairs of stimuli which impinge on two ommatidia separated by two or more intervening ommatidia which are not being stimulated. Hence, cooperation takes place between pairs of ommatidia which are adjacent and between one ommatidium and the next but one.

(c) The maximal optokinetic reaction is elicited by two discrete stimuli which are separated by a time interval $\Delta t \cong \frac{1}{4}$ sec. For smaller as well as larger time differences, the strength of the reaction is less. Minimal reactions are still possible with interstimulus intervals of as much as 10 seconds. Any earlier stimulus which interacts with a later one in a neighboring ommatidium must have some physiologic aftereffect lasting at least Δt seconds; the real interaction must take place between the gradually fading aftereffect (of the first stimulus) and the immediate effect of the second one.

(d) A pair of light stimuli S_{AB}^{++} elicits a response $+R_{AB}^{++}$. The sign before R means that the reaction proceeds in the direction of the stimulus sequence, i.e., from A to B . If the beetle would move freely, this reaction would diminish the relative speed between the environment and the animal.

(e) The pair of dark stimuli S_{AB}^{--} produces the reaction $+R_{AB}^{--}$. We have found that $R_{AB}^{++} = R_{AB}^{--}$.

(f) If one stimulates adjacent ommatidia with the sequence light-dark (S_{AB}^{+-}) or dark-light (S_{AB}^{-+}), optokinetic reactions are elicited which run in direction opposite to the stimulus sequence, i.e., from B to A ; thus, $R_{AB}^{+-} = R_{AB}^{-+} = -R_{AB}^{++} = -R_{AB}^{--}$. If the beetle could move freely this reaction to alternating stimuli would augment the relative speed between the environment and the animal.

(g) Reversal of the direction of the stimulus sequence results in a reversal of the direction of the reaction, thus, $R_{BA}^{++} = -R_{AB}^{++}$; $R_{BA}^{--} = -R_{AB}^{--}$; $R_{BA}^{+-} = -R_{AB}^{+-}$; $R_{BA}^{-+} = -R_{AB}^{-+}$.

(h) Stimulus sequences passing over adjacent ommatidia, e.g. the light stimuli S_{ABCDE}^{+++++} , lead to the response R_{ABCDE}^{+++++} . It became apparent that this reaction is the sum of the partial reactions $R_{AB}^{++}, R_{BC}^{++}, R_{CD}^{++} \dots$ and $R_{AC}^{++}, R_{BD}^{++}, R_{CE}^{++}$. In the same manner $R_{ABCDE}^{+++++} = R_{AB}^{++} + R_{BC}^{++} + R_{CD}^{++} \dots + R_{AC}^{++} + R_{BD}^{++} + R_{CE}^{++} \dots$. Analogous results hold for the sequences S_{ABCDE}^{-----} , S_{ABCDE}^{+----} and S_{ABCDE}^{-+++} .

The experimental results listed under (d), (e) and (f) demonstrate that the

relation between stimulus input and reaction output corresponds to the multiplication of algebraic signs. The result could be summarized as follows:

	S_A^+	S_A^-
S_B^+	$+R$	$-R$
S_B^-	$-R$	$+R$

(i) If the speed of rotation is kept the same, a cylinder consisting of gray sectors in front of a white background produces a weaker optokinetic reaction than a cylinder consisting of black sectors (Hassenstein 1959). Hence, strength of reaction depends not only on the speed of the cylinder but also on differences in reflectance within the pattern. Differences shall be designated as magnitudes. In one of our experiments the stimulus magnitudes was changed by varying the differences in reflectance of the rotating sectors while keeping the speed of the cylinder constant. The background cylinder again consisted of white and black stripes. If the cylinder with gray sectors is rotated, ommatidium *A* receives the stimulus magnitude *x* and ommatidium *B* the stimulus magnitude 1 – *x*, provided one sets the brightness gradient between black and white equal to one. The rotating gray sectors thus produce a sequence of changes in illumination in adjacent ommatidia but leave the sum of stimulus magnitude constant; *x* + (1 – *x*) = 1. The results of the experiment shown graphically in Fig. 4 indicate clearly that strength of response (*R*) is related to the square of the stimulus magnitude, i.e., *R* ~ *x* (1 – *x*). This finding holds for all

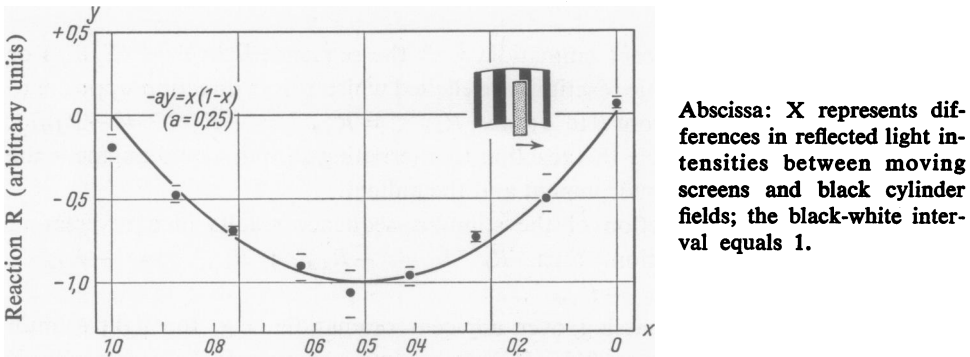


FIGURE 4 Reaction of the beetle to the movement of gray surfaces in front of a black-white background. The beetles saw the pattern of black and white fields (as indicated) through an interrupted cylinder. The narrow slits in that cylinder were separated by the same angular distance as were the white stripes of the background cylinder. Extreme values are indicated by short horizontal lines. The fitted curve has the formula $-aR = x(1 - x)$; *a* was set equal to 0.25, thus making the maximum of the reaction curve equal to -1.

speeds eliciting optokinetic reactions except for very low speeds of the cylinder which produce just measurable reactions. In this range the magnitude of the response depends on that of the stimulus in a more complicated fashion; this is related to processes of adaptation and shall not be discussed here further.

(j) If one stops the rotating cylinder suddenly, the optokinetic reaction of the experimental animal falls slowly to zero. Within 5–8 seconds the reaction drops to about one-third of its original strength.

In summarizing the findings listed under (e), (f) and (i) we can say: strength and direction of optokinetic reactions reflect, in amount and sign, the product of pairs of interacting single stimuli. Between adjacent ommatidia and between one ommatidium and the next but one there must be neuronal connections which multiply amounts and signs of the stimuli received.

The optokinetic turning reaction elicited by sequences of single light flashes depends therefore on separation in time, separation in space, temporal order, magnitude and sign of interacting individual stimuli. If one wishes to gain a picture of the basic working principle of such a complicated process, there is only one way open: the construction of a minimal mathematical model that contains all of the experimental results obtained so far (Hassenstein and Reichardt 1956b). Such a model makes it possible to devise new meaningful experiments and may eventually allow us to predict the reactions to any sequence of stimuli. This was the aim of our further investigations.

The functional diagram of a horizontal section of the eye of the beetle *Chlorophanus*, as shown in Fig. 5, is a summary of the experimental results described in paragraphs (a), (b) and (h). The letters *A*, *B*, *C*, . . . symbolize a row of ommatidia. The connections which have been drawn in, represent information channels, and not actual nerve fibers. Cross connections are situated at the points indicated by dots. The systems marked *P* perform operations upon signals received from pairs of adjacent ommatidia and from any one ommatidium and the next but one. The results of these operations (partial reactions) are summed at stage Σ , thus forming the total reaction strength *R*. If a horizontal section consists of *n* ommatidia, then *R* is composed of $2n - 3$ partial reactions.

The adding of partial reactions and the impossibility to distinguish the *P* systems by experiment have an interesting consequence: If a pattern moves past the upper half of the eye of the beetle *Chlorophanus* at constant speed, the optokinetic reaction is R_1 . If the same pattern is exposed at the same speed to the lower half of the eye, the reaction is R_2 . If one adopts the system of connections portrayed in Fig. 5 for the horizontal section of the compound eye, then $R_1 = -R_2$. Both stimuli moving simultaneously thus, ought to cancel each other; the reaction should be zero. This deduction has been tested in a similar experiment and confirmed.

The functional structure of the *P*-systems can be developed logically from the experimental results given from (c) to (j)—with the exception of those given under

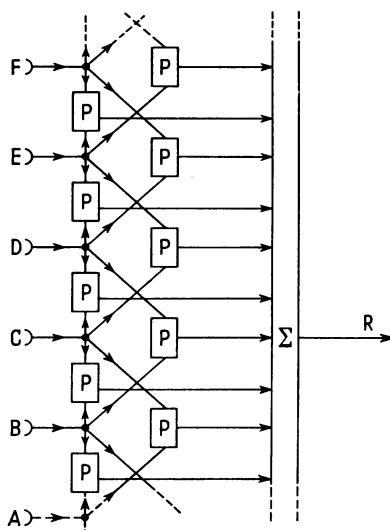


FIGURE 5 Functional diagram of the information channels and computing systems in a horizontal section of the eye of the beetle *Chlorophanus*. The entrances at *A*, *B*, *C*, . . . stand for ommatidia. The connecting lines represent information channels which carry information in one direction only (see arrows). Cross connections exist only at crossings marked by dots. The dashed lines indicate that this figure represents only a segment of a longer row of ommatidia. Processing of information takes place in the system marked "P." Σ represents the stage in which the signals are summed. *R* is the optokinetic reaction according to sign and amount.

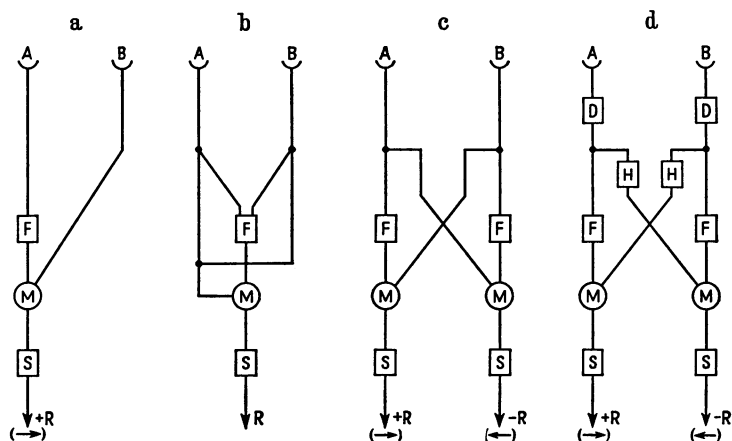


FIGURE 6 Logical development of the minimal model for transfer and processing of information in a double ommatidium system. The connections represent information channels and not nerve fibers. The stages *D*, *F*, *H* and *S* represent transmission processes in the nervous system. The *M* stage combines the transmitted stimulus magnitudes according to sign and amount (and computes the resultant reaction). The development of the different models is discussed in the text.

(h). This development is shown in Fig. 6 and shall be reported here in short: We select a double system consisting of ommatidia A and B and apply first a stimulus to A and then, after Δt seconds, the same stimulus to B . According to paragraph (c) there is an interaction between the aftereffect of the stimulus to A and the subsequent stimulation of B : the result of this interaction depends on Δt . In section a of Fig. 6 the aftereffect is indicated by stage F and the interaction by stage M . The nature of their interaction can be described from the experimental results summarized in paragraphs (d), (e), (f) and (i). Since the interaction is in the nature of an algebraic multiplication, both in regard to sign (direction of stimulus change) and amount (magnitude of stimulus change), " M " stands for the Multiplicative interaction. Finally, the inertia of the optokinetic reaction—according to point (j)—is taken account by inserting stage S .

Optokinetic reactions are elicited not only by a stimulus sequence AB —i.e., first stimulus in A , second in B —but also by the reverse sequence—first stimulus in B , second in A . Not only the signal coming from A but also the one coming from B produces an aftereffect. This consideration leads to model b in Fig. 6. It contains—in its more differentiated section—four connecting channels, i.e., two more than in a . The number of stages F and M is unchanged.

In addition, we have to provide a mechanism for the condition mentioned in paragraph (g): Reversal in the direction of the stimulus sequence results in a reversal of the direction of response. This condition is not fulfilled in model b . One can see immediately that reversing the stimulus sequence has no influence on the sign of the signal which is produced at the exit of the M -stage. Only if one doubles the F - and M -stages does one obtain a model (see part c in Fig. 6), which fulfills this condition and thus possesses a structure which is both "necessary and sufficient" to accommodate all individual findings.

Model c still does not take into account that there can be no transmission in the nervous system without some loss of information. We are trying to take this fact into account by concentrating in D and H the transmission properties of the longitudinal and transverse connections. The final result is model d , which is reproduced separately in Fig. 7.

Let us suppose a brightness gradient (e.g., the transition from white to black) passes over a double ommatidium system A and B , as in the model in Fig. 7. The contour may fall into the visual field of ommatidium A at the time t_0 and into the visual field of ommatidium B at the time $t_0 + \Delta t$. At the exits of stages D the contour produces signals which proceed via the longitudinal connections (past F , with long aftereffect) and the transverse connections (past H , with short aftereffect) to the multiplier stages (M). If Δt is of long duration (more than ten seconds) then neither of the two M stages will emit signals, since no more than one of their input channels will furnish, at any given moment, inputs that are different from zero.

However, if Δt lies within the range of decay periods at the F stages, then the M

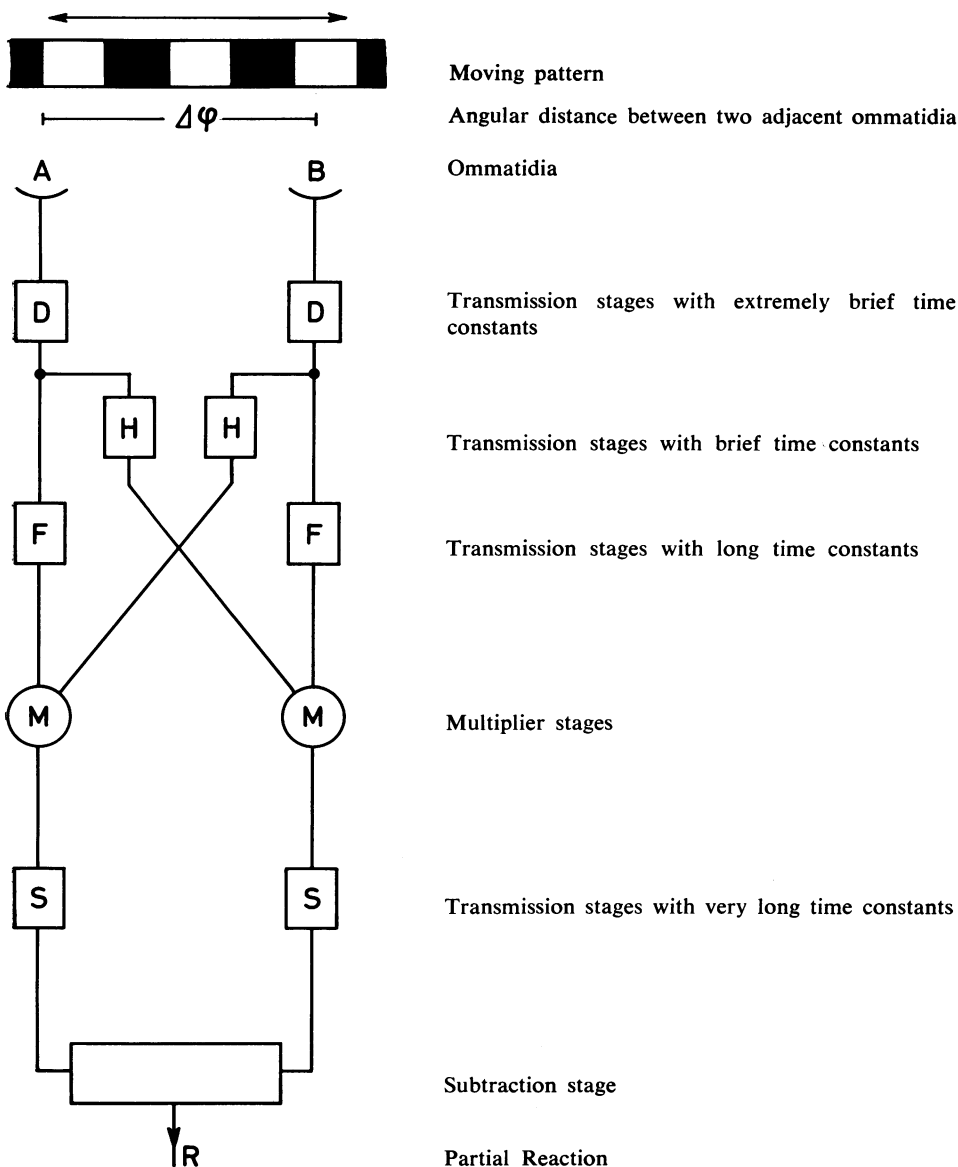


FIGURE 7 Minimal model (dual system involving two ommatidia only) for motion perception of *Chlorophanus*. The ommatidia A and B receive equal values of luminous flux from the pattern which moves with velocity v with relative time delay of $\Delta t = \Delta\phi/v$. A and B thus provide information for the signal channels which feed the multiplier stages M . The M stages react to the amounts of the incoming signals as well as their algebraic signs. The connections in the model thus do not represent neuronal pathways, in any literal sense, since the latter have less capacity for signal transmission. For details see text.

stage at the left receives simultaneous signals (though only for a very short time), from both channels: from *B* via *D* and *H*, as well from *A* via *D* and *F*; from the latter only because of the greater length of the decay period at *F*, and only with a strength corresponding to the aftereffects of *F*. This means that the *M* stage to the left transmits values different from zero only at such times when both of its inputs simultaneously report values that differ from zero. These values depend in part on the strength of the aftereffect which is still present at that moment in the *F* stage to the left.

Because of the short decay period at *H*, the *M* stage to the right does not receive simultaneous signals. This happens only with extremely short Δt , which brings it within the decay period of the *H* stage. However, if a contour moves from *B* to *A*, then we obtain signals from the *M* stage to the right. The resultant at the output of the *M* stage to the left is then equal to zero. The model in Fig. 7 implies, therefore: The greater the velocity of the contour which moves from *A* to *B*, the smaller the Δt ; correspondingly, the less decay in the functional state of the *F* stage to the left (at the time of arrival of the signal from *B*), and the greater, finally, the result of the multiplication, i.e., the stream of signals emanating from the *M* stage to the left. By contrast, if the contour moves from *B* to *A* then the *M* stage to the right has a finite output, while that of the *M* stage to the left is practically zero. The *S* stages in Fig. 7 represent intervening stages for transmission, with time constants of 5–8 seconds. We have symbolized synergistic reactions to contours moving from *A* to *B* (reactions “with”) by the plus (+) sign and those from *B* to *A* by a minus (–) sign. This feature is embodied in the subtraction stage in Fig. 7. The result of the subtraction is the partial reaction of the double system. The minimum model for a double system (involving a pair of ommatidia, see Fig. 7) thus represents a functional arrangement which translates the speed of a moving contour into a functional value and which distinguishes movements occurring from left to right from those occurring in the opposite direction.

The actual kinetics of stages *D*, *F*, *H* and *S* (i.e., their quantitative characteristics of transmission), cannot be derived from what has been said in paragraphs (a) to (j) about reactions to discrete stimulations of ommatidia. We adduced the following experiment on order to determine the character of transmission in these stages: The innermost cylinder (see Fig. 3) had slits with angular distances that exposed only the visual fields of every other ommatidium. The outermost cylinder was removed. The intermediate cylinder with its gray sectors was provided with a one-dimensional pattern, so that its reflectance varied in sinusoidal fashion (see Fig. 8a).

Rotation of the cylinder with the sinusoidal pattern (of that particular wave length of the sinusoid) elicits synergistic reactions (reactions “with”) whose strength depends on the velocity of the cylinder. Fig. 8b indicates the strength of the optokinetic reaction as a function of the angular velocity of the cylinder on a semi-log plot. One sees that the reaction extends over approximately three log units. On

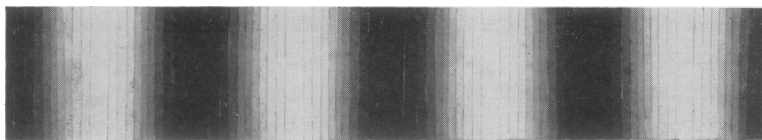


FIGURE 8a Approximately sinusoidal black-white pattern, produced by combination of vertical strips of gray paper of known brightness.

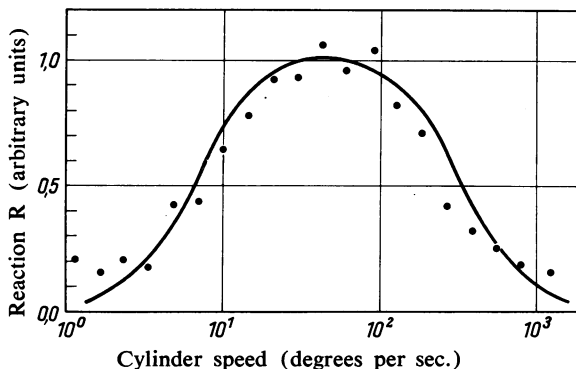


FIGURE 8b Reaction of beetle to movement of a sinusoidal pattern with the periodicity of 66° . The maximum of the reaction is equal to $+1$.

this logarithmic scale, rise and decline are symmetrical to either side of the maximum. This maximum reaction corresponds to a periodic change of illumination in the ommatidia of about one per second.

One can approximate the course of the reaction by drawing a curve (in Fig. 8b) through the experimental points; from this we can determine the kinetics of the transmission stages D , F , H , and S (see Fig. 7). We have found that the transmission characteristics of the D -stages correspond the events which occur in a one-dimensional diffusion process. The time constant of this process is $D \leq 10^{-4}$ sec. The kinetics of the F , H and S stages belong to the same transmission type. They correspond to chemical reactions of the first order (monomolecular reactions) and possess the time constants $\tau_F = 1.6$ sec., $\tau_H = 0.03$ sec., and $\tau_S = 5-8$ sec. With this, the functional characteristics of the double ommatidium system (according to Fig. 7) has been completely determined (Reichardt 1957, Reichardt and Varjú 1959).

The experimental results described thus far have been adduced for the construction of a minimal mathematical model which describes the functional processes in the central nervous system during motion perception in *Chlorophanus*. We now wish to prove that this model allows quantitative prediction of optokinetic reactions to the movements of any kind of cylinder pattern.

At first we proceeded as follows: A one-dimensional cylinder pattern is selected

and mathematically defined. The strength of the optokinetic reaction to different velocities of the pattern can then be calculated in advance on the basis of the minimal model in Fig. 7 which included the relations between (stimulus) input and (reaction) output. The result thus derived by theoretical means is then compared with actual measurements of reactions obtained in the same cylinder. We have done this for a number of different patterns and have found complete agreement between prediction and experiment.

In testing the minimal model for the double ommatidium system (according to Fig. 7) we can use an even stronger criterium: In the central nervous system of *Chlorophanus* there occur two processes which differ fundamentally in their function. In stages *D*, *F*, *H* and *S*, signals are transformed; in the *M* stages, however, signals enter into computations. This computing of signals has a characteristic feature which can be explained in principle in terms of multiplication of algebraic signs. If the inputs of an *M* stage receive simultaneous plus signals, then the signals generate a plus output. The same output of an *M* stage, however, is obtained if both input signals carry minus signs. An "observer" placed at an output of a *M* stage can therefore not decide, when he measures a plus signal, whether this has been produced by combination of two plus or two minus signals at the input side. The situation is analogous when the input of a *M* stage consists of plus-minus or minus-plus combinations. In both instances the resulting output carries a minus sign which precludes any decision as to the nature of the two possible input combinations. This means that the multiplier stages destroy part of the selective information which arrived at their inputs. However, this part of the information is also contained in a moving dark-light pattern which serves to elicit optokinetic reaction. Variations in the pattern which are limited to this portion should have no influence on strength and direction of the response. We postulate, therefore: There exists a class of mathematically distinct dark-light patterns which *Chlorophanus* evaluates as equal with regard to optokinetic reactions (Reichardt and Varjú 1959, Varjú 1959).

First of all we have investigated the mathematical features which characterize this class. It is known that functions can be represented, under very general conditions, according to a theorem by Fourier by a sum of periodic (sinusoidal) series of different wave length, amplitude, and phase relations. If one constructs any dark-light pattern by combinations of such "elementary" functions (Fourier components) then one can demonstrate that changes in the pattern which arise from varying phase relations of these elementary functions should have no influence on strength and direction of the optokinetic reaction. Fig. 9 contains a simple example for this.

We have subjected this quantitative prediction about motion perception of *Chlorophanus* to experimental proof. To this end we used an experimental arrangement which has already been described in connection with reactions to the movement of sinusoidal dark-light patterns. In selecting a pattern for a cylinder, we did not choose the one shown in Fig. 9 which is difficult to produce, but the patterns

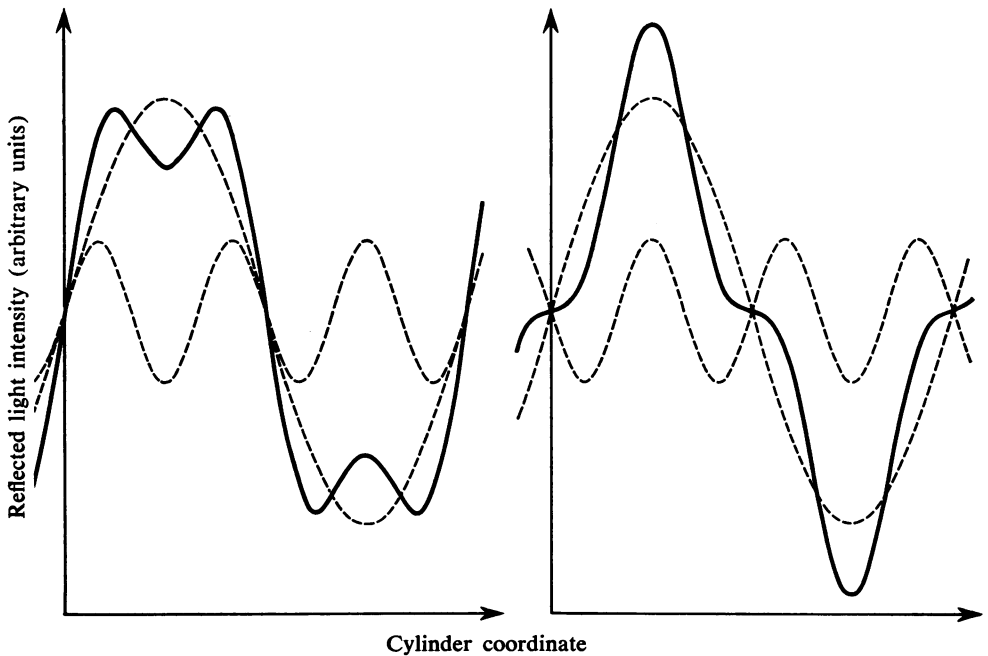


FIGURE 9 Two different dark-light patterns obtained by superimposing two sinusoidal component patterns which differ in phase. The eye of the beetle does not distinguish these patterns, in spite of their essential differences.

C, *D* and *E* from Fig. 10. Patterns *C* and *D* were produced by superposition of the regular black-white patterns *A* and *B*. *A* and *B* in turn, resulted from a sum of sinusoidal periods with different wave lengths, amplitudes, and phases. In synthesizing *C*, patterns *A* and *B* were shifted in relation to one another so that the contours of the longwave pattern fell half-way between the contours of the shortwave pattern. In producing *D*, the contours of the two patterns were superimposed. The difference between pattern *D* and *C* results from shifting *B* in relation to *A* by one quarter wave length. The superimposed patterns *C* and *D* differ, therefore, only with respect to phase relations between the sinusoidal elementary functions which are contained in *A* and *B*.

On the basis of the minimal model for a double ommatidium system (Fig. 7), we have computed (Varjú 1959) direction and strength of the optokinetic reaction as a function of the velocity of patterns *C* and *D*; these predictions were compared with the corresponding actual measurements derived from *Chlorophanus* (Hassenstein 1959). Fig. 11 shows the results. The continuous curve represents the predicted reaction. Circles and dots indicate mean values obtained from different beetles reacting to patterns *C* and *D* respectively. Theory and experiment are in good agreement. The change in the sign of the reaction with increasing velocity of the

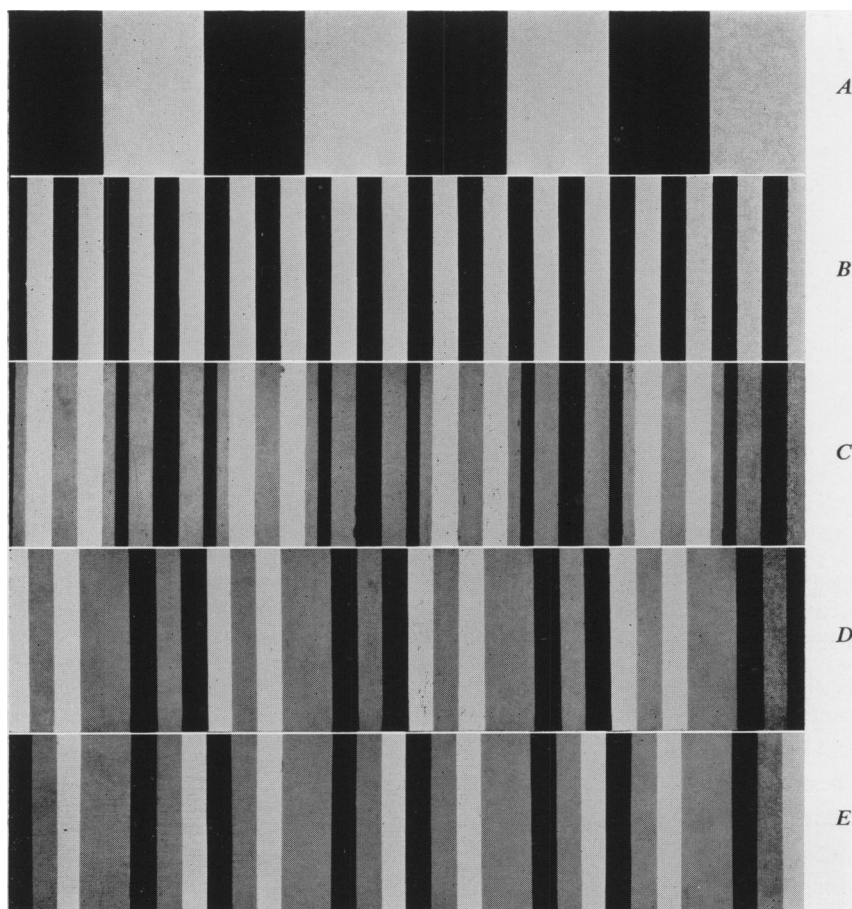


FIGURE 10 From top to bottom: *A*) Periodic black-white cylinder pattern; length of period 90° . *B*) Periodic black-white cylinder pattern, length of period $22\frac{1}{2}^\circ$. *C*) Periodic pattern produced by superimposing *a* and *b*. Before superimposing the patterns, *a* and *b* were shifted relative to one another, so that the vertical contours of the 90° pattern fell halfway between the contours of the $22\frac{1}{2}^\circ$ pattern. *D*) Periodic pattern produced by superimposing patterns *a* and *b*. Before superimposing the patterns, vertical contours of both patterns were made to coincide. The superimposition was performed according to the rules for the mixing of pigments. Accordingly, black + black = black; white + white = white; and black + white = gray. *E*) This periodic pattern was secured from pattern *D* by interchanging two adjacent black-white stripes per period. Pattern *c* and *d* differ from *a* and *b* only by virtue of a phase shift between sinusoidal components.

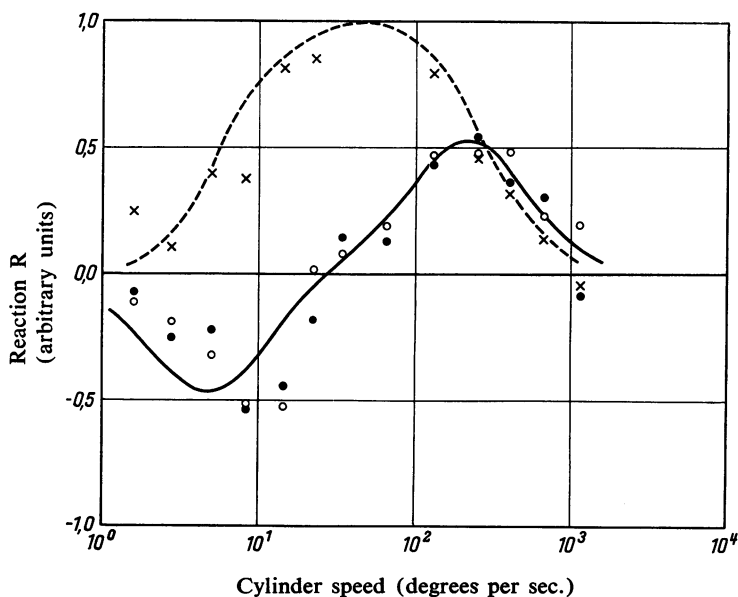


FIGURE 11 Reactions of beetles to movement of the following dark-light patterns: 1) pattern according to Fig. 10c: empty circles; 2) pattern according to Fig. 10d: filled circles; 3) pattern according to Fig. 10e: crosses. The two reaction curves were derived from mathematical predictions based on the minimal model for a double ommatidium system: 1) continuous curve: reactions to patterns 10C and 10D; 2) interrupted curve: reactions to pattern 10E. Maximum of the interrupted curve has been set equal to +1.

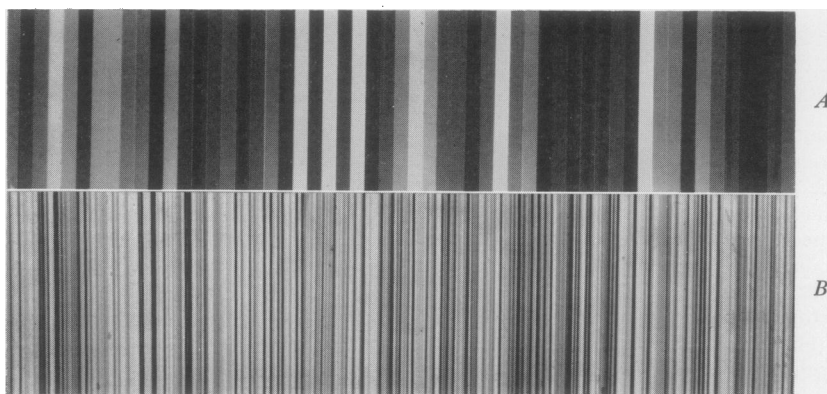


FIGURE 12 Random pattern of stripes (visual noise) for tests cylinders. The order of different shades of gray has been determined by throwing dice. A) stripe-width 7° ; B) stripe-width 1° .

pattern can be accounted for in terms of "geometrical interference effects" between the periodicities of the patterns and of the roster of ommatidia. We have chosen the periodic patterns in such a way that the direction of the reaction should reverse itself with increasing velocity of the patterns.

The experiments with patterns *C* and *D* demonstrate that the optokinetic reaction is not influenced by those portions of the information which are contained in the phase relations of sinusoidal components. One could object at this point that the relatively minor differences between pattern *C* and *D* exert a negligible effect on the reaction, so that both reactions should be approximately equal. That this is not the case, can be shown by the reaction to movement of pattern *E*. Pattern *E* arises from *D*, if one interchanges in *D* two adjacent black-white stripes per period. Pattern *E* can thus *not* be produced by superimposition of *A* and *B*. In other respects it differs only slightly from *D*. The crosses in Fig. 11 represent mean values obtained by measuring reactions to movement of pattern *E* from Fig. 10. The interrupted curve was predicted from the model. One can see from the figure, how drastically a small change in pattern can influence the optokinetic reaction, as long as the change does not fall into the class of changes to which the perception of movement is insensitive.

The light-dark sequences considered thus far are periodic. As soon as one knows one period, the entire pattern is determined. In its natural environment, however, the beetle is surrounded by light-dark sequences of a rather different sort. In general, no part of its visual world recurs periodically. The array of "points" of different reflectance in this natural environment is ruled by statistical and not by analytic laws. The so-called visual noise functions form a limiting case among these statistically "regulated" arrays of points within a pattern (Reichardt 1957). Fig. 12 gives two examples of unidimensional light-dark sequences of this type. Both patterns have been composed by combining stripes of different shades of gray. The order of individual stripes is purely random. The appearance of a particular stripe of gray, at a particular place within the pattern, does not depend on the presence or absence of any particular stripe of gray in its vicinity, or anywhere else in the pattern. The periodic patterns represent the limiting case of complete order; the noise functions represent extreme disorder. The light-dark sequences in the visual world of the beetle fall between these two extremes.

We ask the following question: Do optokinetic reactions depend for their elicitation on the movement of dark-light sequences which possess figure character and are thus orderly, or is it possible to obtain such reactions from patterns of the type of the visual noise functions (Fig. 12) which possess contrast but are devoid of figure character? To answer this question, we prepared cylinders with the patterns 12a and 12b, and measured the strength of the turning reaction of *Chlorophanus* as a function of the velocity of the cylinder (Hassenstein, 1958 a, 1959). Fig. 13 shows the result of these investigations. The dots show mean values obtained with cylinder 12a, the crosses, mean value for movement of pattern 12b. The continuous

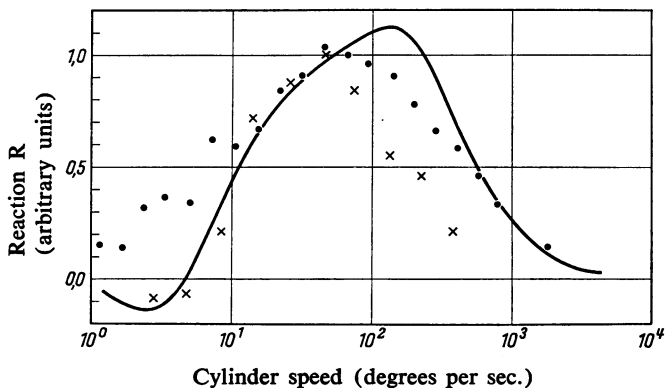


FIGURE 13 Reaction of beetle to the movement of random patterns of stripes: 1) pattern according to Fig. 12a: dots; 2) pattern according to Fig. 12b: crosses. The maxima of the actual reaction, as measured, have been set equal to one.

reaction curve has again been calculated in advance on the basis of the minimal model in Fig. 7 (Reichardt and Varjú 1959). This calculation is based on two assumptions which can only be realized very approximately in the experiment. According to the first assumption, the width of the stripes of gray is supposed to be infinitely small. The second assumption bases the calculations on a statistical pattern of stripes which does not recur periodically in sections, as is inevitable if one uses a cylinder. Accordingly, good agreement between the predicted curve and the actual measurements is found only within the range of increasing strengths of reaction to the cylinder, as pattern 12b moves past the array of ommatidia. Pattern 12b conforms considerably better than pattern 12a to the assumption of shades of gray of differential width (i.e., non-recurrent). The effect of the periodicity of the cylinder becomes manifest with velocities above 60° per sec. The course of the reactions to very low velocities of the cylinder should also be noted. We found, by experiment (with pattern 12b) and on the basis of theory, that here the reaction should have a direction opposite to that of the movement of the pattern. A more detailed investigation has revealed that this behavior is caused by the transmission characteristics of the *D* stages.

The result, viz. that moving random patterns elicit optokinetic reactions in *Chlorophanus*, can be derived qualitatively from the minimum model of a double ommatidium system for movement perception. To this end, we consider the statistical attributes of the signals entering the *M* stages, if a random light-dark pattern moves past the ommatidia from left to right. Two possibilities have to be kept in mind in this connection: First, the aftereffects at the *F* stages (and all the more at the *H* stages) might be so evanescent in relation to the velocity of the moving pattern that all aftereffects of a particular stimulus arriving from ommatidium *A* have

disappeared at stage *F* by the time the same stimulus arrives in ommatidium *B*. In that case the relations between the signals that enter the two multiplier stages are a matter of pure chance, since the shades of gray in the light-dark pattern itself are likewise statistically independent of one another. Signal combinations entering the *M* stage and announcing light-light, dark-dark, light-dark, dark-light are equally probable and, hence, on the average, for longer periods, equally frequent; every combination appears in 25% of all cases. Different situations arise, if the duration of aftereffects at stage *F* becomes similar to the time spent by a point in the pattern in travelling from ommatidium *A* to ommatidium *B*. Let us assume that *B* receives a particular stimulation before the aftereffect of the same stimulation transmitted from *A* to the *F* stage, has disappeared at *F*. For instance, if the signal in *B* contains information about an increase in light intensity then its after-effect persists at the *F* stage which is supplied from *A*; and this persistent effect contributes part of the information represented at *F*. The corresponding is true for a signal carrying information about a decrease in light intensity. It is thus no longer true—as in the first instance—that all portions of concurrently entering signal combinations at the *M* stages are statistically independent. On the contrary, signal combinations produced by light-light and dark-dark stimulation now contribute more to the total input into the multiplier stage to the left, that would correspond to a chance distribution, that is, more than 50%. On the other hand, practically nothing is changed for the input of the *M* stage to the right (as long as we continue to consider a movement of the pattern from left to right). The reason is that the time constants of the *H* stages are considerably smaller than those of the *F* stages. How big is the proportion of coincident signals, in excess of 50%, for the inputs into the *M* stage to the left? The answer depends on the velocity with which the light-dark pattern moves in relation to the ommatidia. As the velocity increases there is a corresponding decrease in the length of the interval between the two identical changes in illumination, which are produced by a point in the light-dark pattern, first in *A* and then in *B*. The after-effects of stimulation do not persist indefinitely with constant strength; they decay. This means that the greater the velocity of the noise visual pattern, the less the decay of the aftereffects of stimulation received at stage *F*, from *A*, at the instant when the corresponding stimulus arrives at *B*. The input of the *M* stages to the left shows therefore a greater proportion of coincident signals, as compared with a chance distribution, when the velocity of the light-dark pattern is high, and a smaller proportion, when the velocity is low. The magnitude of this quantitative excess of coincidence of messages bearing on signals of equal sign is thus an expression of the relative velocity of the moving random pattern.

The considerations, thus far, deal with stimulus reception and transmission through the *D*, *F*, and *H* stages. The evaluation of the signals, and thus the actual “process of measurement”, takes place at the *M* and *S* stages. It turns out that these stages represent a functional arrangement which is particularly apt to yield, as a

direct result of computation, the just-mentioned quantitative excess of coincident signals elicited by stimuli of equal sign, over and beyond a chance distribution. Messages corresponding to combinations light-light, dark-dark, light-dark and dark-light are equally frequent, on the average, as we have shown, as long as the velocity of the pattern is very low. Under these conditions, plus and minus signals are likewise equally frequent within the resulting output of the M stages. This series of signals is averaged by stage S with its great inertia; the output of that stage results in a stream of signals equal to zero, and this corresponds to a reaction of zero strength. If one now increases the velocity of the pattern, then the equal distribution of the four combinations is shifted in favor of a quantitative excess of signals corresponding to light-light, dark-dark stimulation at the entrance of a multiplier stage. In the case of movement from left to right this excess appears at the entrance to the M stage on the left; in the case of movement from right to left, the excess appears at the entrance of the M stage on the right. Signal combinations corresponding to light-light and dark-dark stimuli produce a positive output at the exit from a multiplier stage; the quantitative excess of these combinations therefore result in an excess of positive over a negative flow of signals. After this statistical series has been averaged by one of the S stages, one obtains at the exit of that stage a net outflow of positive signals. The strength of this flow of signals depends on the velocity of the moving pattern and on the direction of its movement.

It has thus been shown that the functional arrangement of a double ommatidium system represents an apparatus for the measurement of seen movements which does not depend on the appearance of figural components in the moving patterns. The evaluation of the transformed stimuli for movement takes place within arrangements of neurones which function in analogy to the algebraic operations of multiplying and averaging. In mathematics, this combined operation is classified as a "first order correlation". Correlation has thus been shown to be an evaluation principle in the central nervous system of *Chlorophanus*.

NEURAL INHIBITION IN FACET EYES

The resolving power of facet eyes usually corresponds to the smallest angles between the optical axes of adjacent ommatidia (Hecht und Wolf 1929). This has been verified again in *Chlorophanus* (Hassenstein 1951, Varjú 1959) and has lead us to the conclusion that the effective visual fields of adjacent ommatidia do not overlap. On the other hand, it has been shown that in many facet eyes light from a point source is absorbed not by the rhabdom of only one but by those of many ommatidia (De Vries, 1959). In addition the diameters of single facets are in many eyes so small that diffraction alone would produce an overlap of the visual fields. These findings are obviously in conflict with each other. However, they can be explained on the basis of neural inhibition.

Cajal and Sánchez (1915) found in *Calliphora* and more recently Mayer (1951)

in *Musca domestica* that a plexus of lateral fibers connects the receptors in the facet eye. The functional properties of these fibers are unknown in *Calliphora* and *Musca*; however lateral connections have been found and carefully studied in the horseshoe crab *Limulus polyphemus* (Hartline 1947, 1952, 1956, 1957, 1958, 1959 and Ratliff 1957, 1958, 1959). The light intensity received by one ommatidium of the *Limulus* eye is absorbed in the rhabdom structure. The absorbed energy generates a potential in one of the retinula cells—the eccentric cell. Under stationary conditions the generator potential of the eccentric cell is logarithmically related to the intensity of the absorbed light while the spike-frequencies in the associated fiber of the optic nerve are linearly dependent on the generator potential. This holds for any of the nerve fibers as long as only one receptor is illuminated. If two or more receptors are stimulated the excitations in fibers of the optic nerve inhibit each other. The interaction is a linear process as long as the excitation in each receptor is greater than the sum of inhibitions, which is usually the case. It has been shown that the lateral fibers are responsible for the inhibitory processes. The strength of mutual inhibition decreases as the distance between the receptors increases.

Using these experimental results of Hartline and Ratliff one may write a set of linear algebraic equations that describes the effect of neural inhibition on the relation between generator potentials and spike frequencies in the optic nerve. The elements of the resulting transformation matrix are the inhibition coefficients. The inverse of this matrix when applied to the generator potentials of the eccentric cells gives the spike frequencies in the optic nerve.

One of the consequences of this neural transformation is that contrasts in the light intensity distribution across the receptor mosaic are exaggerated in the spike frequency distribution. An intensity step on the receptors for instance produces an exaggerated step of excitations across the optic nerve (Mach-Bands). If the visual fields of adjacent ommatidia in *Limulus* did not overlap the neural inhibitions would just increase the contrasts of the light distributions in the optical surroundings. This however is definitely not the case since the visual fields of ommatidia in *Limulus* overlap strongly (Waterman 1954). It can be shown that this process of overlap can also be described mathematically by a set of linear algebraic equations. The elements of the transforming matrix are the coefficients which describe the overlap of the visual fields. In spite of the fact that the generator potentials are logarithmically dependent on the light intensity their relation is well approximated by a linear one. The reason for this is two-fold: The ratio of reflected light intensities in the optical surroundings does not cover a large dynamic range. This range is still smaller in a typical light intensity distribution on the receptor mosaic, since overlap of visual fields smooth out sharp contrasts. With respect to light intensity modulation the image forming process of the facet eye can therefore be described by two sets of linear transformations (Reichardt 1961). The first of these transformations—due to geometric optics—is reversed partly or completely by the second one which is

carried out by neural inhibition. Most interesting is the case when the overlap coefficients equal the inhibition coefficients. Under these circumstances the optical surroundings are perfectly portrayed on the cross-section of the optic nerves, irrespective of whether the overlap is due to the dioptric apparatus of the facets or to diffraction. In Limulus this is the case when a pattern is located a short distance from the eye. Under these circumstances the resolving power of the eye is limited only by the number of receptors.

Fig. 14 contains a model which simulates the principle of neural inhibition and its linear influence on the resolving power of facet eyes. In Fig. 14a the formation

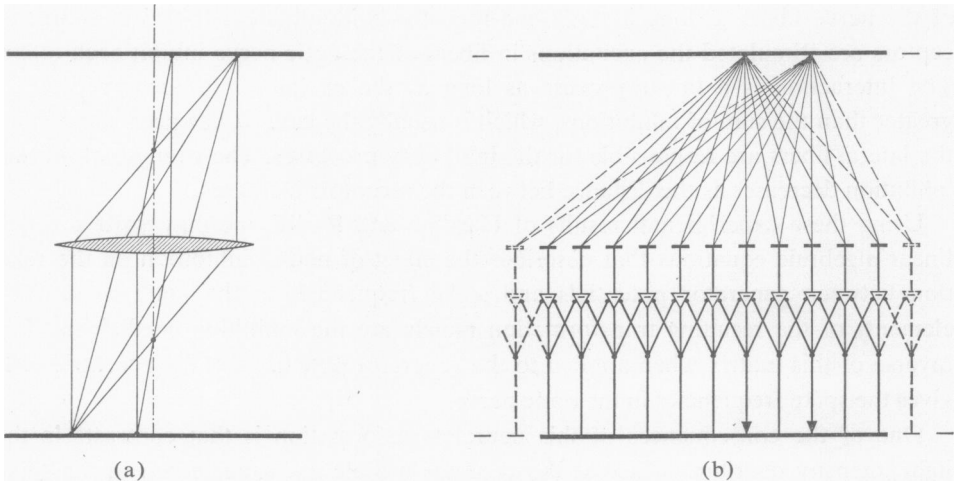


FIGURE 14a Image formation by a lense. b Image formation by the principle of lateral inhibition. Explanation in the text.

of the image of two point sources of light by a lens is shown. The same can in principle be achieved by the model in Fig. 14b. The intensities of two light sources are received by an array of photocells. Each photocell is assumed to have a broad spatial sensitivity distribution. The outputs of the photocells feed the inputs of operational amplifiers. The output of each amplifier is connected to the inputs of all other amplifiers (in Fig. 14b only neighbour connections are shown). Every back connection contains a potentiometer by which the inhibitory coefficient is adjustable. If the inhibitory coefficients equal the overlap coefficients the optical surroundings of the model are imaged onto the outputs of the operational amplifiers. This is indicated in Fig. 14b by the arrows in two of the output lines. These outputs only carry a voltage proportional to the intensities of the light sources. Every other output is zero.

These findings can be summarized as follows: The functional mechanism of

lateral inhibition is in principle able to create an image of the optical surroundings in the optic nerve and can compensate for the dioptric apparatus in front of the receptor mosaic.

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